Evidence for a Tradeoff Between Retention Time and Chewing Efficiency in Large Mammalian Herbivores

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Running head: Particle size and digestion in herbivores

Abstract

Large body size is thought to produce a digestive advantage through different scaling effects of gut capacity and food intake, with supposedly longer digesta retention times in larger animals. However, empirical tests of this framework have remained equivocal, which we hypothesize is because previous comparative studies have not included digesta particle size. Larger particles require more time for digestion, and if digesta particle size increases with body mass, it could explain the lack of digestive advantage in larger herbivores. We combine data on body mass, food intake, digesta retention and digestibility with data on faecal particle size (as a proxy for digesta particle size) in 21 mammalian herbivore species. Multiple regression shows that fibre digestibility is independent of body mass but dependent on digesta retention and particle size; the resulting equation indicates that retention time and particle size can compensate for each other. Similarly, digestible food intake is independent of body mass, but dependent on food intake, digesta retention, and particle size. For mammalian herbivores, increasing digesta retention and decreasing digesta particle size are viable strategies to enhance digestive performance and energy intake. Because the strategy of increased digesta retention is usually linked to reduced food intake, the high selective pressure to evolve a more efficient dentition or a physiological particle separation mechanism that facilitates repeated mastication of digesta (rumination) becomes understandable.

Key words: herbivory, digestion, retention, mastication, metabolism, rumination

Introduction

Mammalian herbivores are thought to facilitate niche separation by the so-called Jarman-Bell-principle (Bell 1971; Geist 1974; Jarman 1974). This principle suggests that larger species can feed on diets of lesser quality (i.e., higher fibre content). The proposed mechanistic background of this concept is the fact that whereas metabolic requirements and hence food intake scales to body mass$^{0.75}$, gut capacity scales linearly to body mass; in other words, the amount of food ingested decreases per unit gut capacity, which should in theory lead to an increase in digesta retention time with increasing body mass (Parra 1978; Demment and Van Soest 1983; Demment and Van Soest 1985; Illius and Gordon 1992; Clauss et al. 2007a). Because digesta retention is a major determinant of digestibility, large body size has been suggested as a major digestive advantage and thus as one of the drivers of Cope's rule in herbivores (Demment and Van Soest 1985). Additionally, the Jarman-Bell-principle has been suggested to facilitate intraspecific niche separation in sexually dimorphic ungulates (Barboza and Bowyer 2000).

Because of the perceived relevance of digesta retention, numerous studies have investigated this parameter, often in conjunction with digestibility measurements (reviewed in Clauss et al. 2007a). However, attempts to correlate digestive efficiency or digesta retention with body mass have remained unsatisfactory for at least three reasons. First, no systematic increase of either parameter with body mass could be demonstrated across species (Justice and Smith 1992; Pérez-Barberìa et al. 2004; Clauss and Hummel 2005; Clauss et al. 2007a). Second, differences in digestive efficiency between sexes of dimorphic species are either absent or low (Gross et al. 1996; Pérez-Barberìa et al. 2008). Third, it is felt that ruminants need to be considered separately from other herbivores due to their higher digestive efficiency (Illius and Gordon 1992), a preconception which prevents a unifying framework for herbivory.

65 While the concept that digesta retention increases with body size (Demment and Van
66 Soest 1985; Illius and Gordon 1992) is only weakly supported by empirical evidence so far
67 (Clauss et al. 2007a), the concept that chewing efficiency decreases (i.e., digesta particle size
68 increases) with body mass (Pérez-Barberìa and Gordon 1998) is clearly corroborated in
69 comparative studies (Udén and Van Soest 1982; Clauss et al. 2002; Fritz et al. 2009). The
70 relevance of reducing the particle size of ingested food is well understood, particularly in
71 herbivores (Clauss and Hummel 2005); specifically, smaller food particles can be digested at
72 a much faster rate. Therefore, many authors have speculated that an increase in chewing
73 efficiency permits shorter digesta retention times, or that – vice versa – longer digesta
74 retention can compensate for a reduced, or even lacking, chewing efficiency. This tradeoff has
75 been evoked for comparisons between chewing and non-chewing dinosaurs (Farlow 1987;
76 Sander and Clauss 2008), between reptiles and mammals (Karasov et al. 1986), between
77 different large mammalian hindgut fermenters (Clauss et al. 2005), between ruminant and
78 non-ruminant foregut fermenters (Schwarm et al. 2009), or between the sexes of a dimorphic
79 ruminant species (Gross et al. 1995). However, a statistical demonstration of such a
80 compensating effect across species has not been presented so far, most likely because data on
81 digestibility, digesta retention and digesta particle size was not available for a suffficiently
82 large dataset (Schwarm et al. 2009).
83 Here, we use the most comprehensive dataset from one single trial on food intake,
84 digesta retention and digestive efficiency in large grazing mammals fed grass hay (Foose
85 1982), and add our own data on digesta particle size (from Fritz et al. 2009) determined for
86 the same species by wet sieving analysis of faeces. We use conventional and phylogeny-based
87 methods to investigate the scaling of digestive traits with body mass and to test two
88 predictions. First, we predict that fibre digestibility is mainly influenced by digesta retention
89 time and digesta particle size (and not by body mass). Second, we predict that energy intake is
90 dependent on overall food intake, digesta retention, and digesta particle size (and not on body

91 mass). We examine variation in a phylogenetic and statistical context that enable us to
92 examine evolutionary change in two or more traits.
93
94 **Methods**
95 The dataset of Foose (1982) was used, which stems from feeding trials of non-domesticated
96 herbivores held in captivity (Appendix). These trials were performed nearly forty years ago
97 (1970-1980). We used data for a grass hay-only diet from species adapted to grazing. This
98 resulted in exclusion of the tapirs, the giraffe, the black rhinoceros and the pygmy hippo from
99 the original dataset, as browsing species have been reported to have difficulties in grass hay
100 ingestion (Clauss et al. 2008a) and/or to produce larger faecal particles in captivity as
101 compared to the wild (i.e., on their natural food) (Hummel et al. 2008). Thus, the data set
102 includes ruminants and camels ("ruminants", n=12), elephants, rhinoceroses and equids
103 ("hindgut fermenters", n=8) and the hippopotamus ("nonruminant foregut fermenter", n=1).
104 The animals were adult and not lactating or pregnant beyond the first month (Foose 1982, p.
105 69). Data were available for body mass (kg), relative organic matter intake ($g/kg^{0.75}/d$), mean
106 retention time (MRT, h), and the apparent digestibility of organic matter and neutral detergent
107 fibre. Data on faecal (=digesta) particle size (mm) was gained from captive individuals of the
108 same species kept in European zoos (from Fritz et al. 2009).
109 For all analyses, body mass and particle size were log-transformed to better meet the
110 statistical assumptions, and we used two-tailed tests with a 5% significance level (α=0.05).
111 For non-phylogenetic analyses, data were analyzed by correlation analysis using SPSS 16.0.1
112 (SPSS Inc., Chicago, IL, USA). To analyze results in a phylogenetic context, we used
113 phylogenetic generalized least squares (PGLS) (Pagel 1997; Pagel 1999). For this, we used
114 the program BayesTraits (Pagel and Meade 2007) to calculate likelihood statistics under
115 models of correlated or uncorrelated evolution. We calculated the parameter λ, which was
116 used to assess whether traits show evidence for phylogenetic signal (Freckleton et al. 2002).

Values of λ close to one indicate the existence of phylogenetic signal, and we used a likelihood ratio test to compare the likelihoods of models when λ was estimated to models in which λ was forced to be zero, as described in Freckleton et al. (2002). Forcing λ to equal zero is equivalent to a non-phylogenetic test. We also used BayesTraits to implement a multiple regression model. Phylogenetic analyses were based on a recent estimate of mammalian phylogeny (Bininda-Emonds et al. 2007).

Results

Scaling with body mass

Results involving the phylogenetic scaling of four measures of digestive physiology with body mass are presented in Table 1. In all cases, we found significant phylogenetic signal (λ close to 1 and significantly different from zero), and results from phylogenetic and non-phylogenetic analyses were consistent. We thus present bivariate plots and results of non-phylogenetic analyses in Figure 1 and statistical results from phylogenetic analyses in Table 1.

Digesta retention time was not significantly related to body mass (Fig. 1a), but faecal particle size increased with body mass (Fig. 1b). Given these two first findings, one would expect fibre digestibility to decrease with body mass, but no significant association was found (Fig. 1c); instead, fibre digestibility appears to be higher in ruminants. Body size was also neither correlated significantly with relative organic matter intake (Fig. 1d) nor with relative digestible organic matter intake (Fig. 1e). In our dataset, the intake of digestible organic matter (i.e., the product of organic matter intake and organic matter digestibility) can be considered as a good proxy for energy intake. Because we limited our dataset to only species that readily accepted the offered diet (grass hay), and because no weight loss was evident during the trials in these species (Foose 1982), this relative digestible organic matter intake represents relative maintenance energy requirements (expressed on a metabolic body weight-

143 basis). Fig. 1e therefore indicates that differences in maintenance energy requirements and
144 hence metabolic rate do occur between different large herbivore species, similar to variation
145 in metabolic rates reported in smaller mammals (McNab 2008).
146
147 *Determinants of fibre digestion*
148 Fibre digestibility increases with digesta retention time (likelihood ratio test: χ^2=10.6,
149 p=0.001, λ=0.9; Fig. 2a), again at generally higher levels in ruminants. Across all species,
150 fibre digestibility decreases with increasing faecal particle size (Fig. 2b), but this result was
151 not significant after controlling for phylogeny (likelihood ratio test: χ^2=2.00, p=0.16, λ=1.0).
152 We also used PGLS to run a multiple regression analysis with fibre digestibility as the
153 dependent variable and digesta retention time, faecal particle size, body mass and relative
154 organic matter intake as independent variables. The model explained a large proportion of the
155 variation in fiber digestibility (R^2=0.89), and the maximum likelihood estimate of λ was 0
156 (equivalent to a non-phylogenetic test). The model produced significant effects for only
157 digesta retention time and particle size (Table 2). As the regression coefficients for these two
158 variables had opposite signs, this is consistent with a compensating effect of these two
159 variables. Based on the high λ's in the bivariate tests, we re-ran the multiple regression with λ
160 set to 1 (R^2=0.58). The results again demonstrated significant (and opposite) effects for
161 retention time and particle size (Table 2).
162
163 *Determinants of energy intake*
164 In order to test for the relevant factors that influence energy intake, and allow a higher relative
165 metabolic rate in a species, we ran a second multiple regression analysis, with relative
166 digestible organic matter intake as the dependent variable, and body mass, relative food
167 intake, retention time and particle size as independent variables. Although the result could be
168 considered self-evident because the dependent variable (relative intake of digestible material)

is a product of the independent variables (relative intake and the factors shown to determine digestibility), this analysis is important because it is the overall intake of digestible material (i.e. energy) that is the currency relevant for the energy budget of the organism, not digestibility itself; actually, the goal to achieve a high digestibility may set a constraint on intake (Clauss et al. 2007b).

As in the previous multiple regression model, the maximum likelihood estimate of λ was 0, and a high proportion of the variation was accounted for by the model (R^2=0.97). Relative organic matter intake was a highly significant predictor of relative digestible organic matter intake. Body mass was not statistically significant (Table 3). Digesta retention time was also statistically significant, and faecal particle size approached significance. We repeated the analysis with λ=1 (R^2=0.90). In this analysis, only relative food intake was statistically significant, although digesta retention approached significance (Table 3).

Discussion

In contrast to the common assumption in the literature (Demment and Van Soest 1985; Illius and Gordon 1992), we found no evidence that an increase in body mass confers a digestive advantage. The absence of an effect is unlikely to be due to insufficient variation in body mass, as our dataset included species that ranged from 133 to 3402 kg. Instead, the results suggest that to increase digestive efficiency, herbivores either increase digesta retention, or enhance chewing efficiency, or both (or select a diet of higher digestibility, an option not open for most larger-sized herbivores). In comparison to earlier herbivore digestion models (Demment and Van Soest 1985; Illius and Gordon 1992), digesta particle size thus becomes an important variable for understanding digestive adaptations in herbivores. Actually, the lack of consideration that digesta particle size received in earlier concepts might explain why they remain unsatisfactory when applied to mammalian data. The strong phylogenetic signal detected in our analyses indicates that the parameters investigated – mainly digesta retention

and particle size – have played a fundamental role in the evolution of different mammalian large herbivore groups; actually, these results underline the impression already evident from the graphical depiction of the data (Fig. 1-3) that differences in digestive strategy are at the core of the phylogenetic differentiation of large herbivores. The fact that both digesta retention time and faecal particle size show a strong phylogenetic signal, but only particle size shows a significant correlation with body mass after accounting for phylogeny (Table 1), could indicate different constraints on these two parameters – namely that whereas animal lineages might evolve retention times independent of their body size (Clauss et al. 2007a), evolutionary strategies used so far could not completely liberate digesta particle size from the constraining effect of body mass (Fritz et al. 2009). A likely explanation for this interpretation is that tooth size and chewing frequency are both allometrically correlated with body mass (Shipley et al. 1994; Pérez-Barberìa and Gordon 1998).

In order to evolve the potential for a higher metabolism, i.e. a higher energy intake, herbivore species should, above all, increase food intake, but should also increase digesta retention in the gut, and reduce digesta particle size. Because an increase in digesta retention is, among large mammals, not the automatic result of an increase in body mass, there appear to be two major strategies to increase digesta retention: an increase of gut capacity or a reduction in food intake (Clauss et al. 2007a). Both of these strategies imply conceptual disadvantages that might limit the scope of adaptation that can be derived from an increase in digesta retention time.

Increasing the relative capacity of the gut might constrain, by volume displacement, the function of other organs. For example, Clauss et al. (2003) and Mortolaa and Lanthier (2005) independently speculated that the high water content in the faeces of large cattle-like ruminants (defecating in ‘pies’), or the observed unusually high breathing frequency in this group of ruminants, could be the result of a space competition between organs in the body cavity, with the particularly voluminous forestomach in these animals reducing the space

available for the organs of water-reabsorption from digesta (colon) or air exchange (lung), respectively. Additionally, increasing gut capacity might ultimately limit the agility of the animal, and therefore, particularly high gut capacities might only be an option for animals that are, due to their ecology or body size, relatively immune to predation, such as hippopotamids or sloths. Yet, gut capacity might be, across vertebrate herbivores, more flexible than one would expect based on mammal data alone: in herbivorous dinosaurs such as stegosaurs, ankylosaurs, or sauropods, relative gut capacities exceeding the ones in mammalian herbivores have been suggested to facilitate long digesta retention to compensate for a lack of chewing mechanisms (Bakker 1986; Coe et al. 1987; Franz et al. 2009).

Food intake was negatively associated with digesta retention in our dataset (Fig. 3). A negative association between food intake and digesta retention follows the common-sense logic that an increased input into a tube will result into an increased output and a shorter passage time; this association has been found both within and between species (Clauss et al. 2007a; Clauss et al. 2007b). Among primates, this relationship was also demonstrated using phylogenetically independent contrasts (Clauss et al. 2008b). In our dataset, however, this relationship was not significant in a phylogenetic test (likelihood ratio test: χ^2=0.1, p=0.75). This can be explained by the taxonomic clustering of data along these dimensions (see Figure 3): while artiodactyls (hippopotamus and ruminants) cluster at the low-intake, long-retention end, perissodactyls and elephants cluster at the high-intake, short-retention end of the spectrum. This finding again emphasizes that alternative digestive strategies were a major determinant of lineage diversification in large mammalian herbivores. Nevertheless, the evolutionary option to increase energy gain by increasing digesta retention is potentially constrained by the consecutive, necessary reduction in overall food intake.

The only non-ruminant foregut fermenter in this dataset, the hippopotamus, is a good example of the strategy of particularly long retention times due to a low food intake and an enormous gut capacity (Clauss et al. 2003; Clauss et al. 2004; Clauss et al. 2007b). Due to the

247 obligatory low food intake on this long-retention strategy, hippos are characterized by
248 remarkably low maintenance energy requirements (Schwarm et al. 2006). Apparently, the
249 range of adaptation possible due to increased digesta retention is limited to comparatively low
250 energy requirements and low metabolic rates. Among other mammals, this strategy is
251 common among non-ruminant foregut fermenters and some small hindgut fermenters (Clauss
252 et al. 2007a; Clauss et al. 2008b; Munn et al. 2008).

253 On the other hand, there are two major strategies to increase chewing efficiency and thus
254 reduce digesta particle size: by evolving a more efficient dental design, or by increasing the
255 time spent chewing per unit digesta (i.e., rumination). The prerequisite for efficiently
256 increasing the time spent chewing per unit digesta is a sorting mechanism that separates
257 smaller from larger particles (Fritz et al. 2009; Schwarm et al. 2009). Rumination sets a
258 constraint on food intake, because it represents a relevant proportion of the activity budget
259 that can therefore not be used for feeding (Van Soest 1994). Due to this strategy of repeated
260 mastication and moderately long digesta retention, ruminants are thus limited in the amount of
261 food they can ingest (Fig. 1d); but due to the exceptional small digesta particle sizes they
262 achieve (Fig. 1b), they can attain disproportionately high digestibilities for their digesta
263 retention (Fig. 2a). The equids of our dataset represent the strategy of a particularly
264 sophisticated dental design (Jernvall et al. 1996; Fritz et al. 2009) that allows a high degree of
265 digesta particle size reduction (Fig. 1b) without a constraint on food intake. Thanks to their
266 efficient teeth, equids can afford a high food intake and still respectable digestive efficiencies,
267 which potentially allows them higher intakes of digestible matter and energy than ruminants
268 (Foose 1982; Duncan et al. 1990).

269 Increasing digesta retention will increase digestive efficiency; however, it will, in varying
270 degrees between species, also limit food intake. Increasing chewing efficiency therefore
271 appears as an attractive alternative to enhance energy uptake. This implication explains the
272 high selective pressure on mammals to acquire more efficient dental designs if they were to

fuel organisms of increasing metabolic scope (Reilly et al. 2001) – because the adoption of a more efficient dental design is ultimately the only strategy to enhance digestive efficiency without compromising food intake. In order to fully understand the ecophysiological diversification of herbivores, not only gut capacity, food intake, and digesta retention, but also ingesta particle size reduction must be taken into consideration.

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Appendix

Dataset used in this study

Species		Digestion type	Body mass[1]	Organic matter intake[1]	Mean retention time[1]	Organic matter digestibility[1]	Fibre (NDF) digestibility[1]	Mean particle size[2]
			kg	$g/kg^{0.75}/d$	h	%	%	mm
Cervus duvauceli	Berasingha	Ruminant	193	40	52.0	56.33	54.91	0.219
Cervus elaphus	Red deer	Ruminant	284	39	62.0	48.39	51.92	0.471
Kobus ellipsiprymnus	Waterbuck	Ruminant	204	64	62.0	49.23	52.36	0.385
Oryx gazella	Gemsbok	Ruminant	204	71	75.0	53.72	55.35	0.280
Tragelaphus oryx	Eland	Ruminant	454	47	57.0	52.93	49.82	0.704
Boselaphus tragocamelus	Nilgai	Ruminant	193	48	61.0	52.55	53.09	0.708
Bison bison	American bison	Ruminant	408	57	78.0	62.34	64.51	0.450
Bos frontalis	Gaur	Ruminant	816	50	64.0	58.62	58.82	0.399
Bubalus bubalus	Water buffalo	Ruminant	635	71	79.0	58.86	58.74	0.609
Syncerus caffer	African buffalo	Ruminant	280	67	76.5	64.46	64.90	0.465
Camelus dromedarius	Dromedary	Ruminant	544	42	78.5	61.03	62.36	0.444
Camelus bactrianus	Bactrian camel	Ruminant	544	42	88.0	61.81	62.26	0.566
Hippopotamus amphibius	Common hippopotamus	Foregut fermenter	2268	42	92.0	54.88	51.94	17.807
Equus grevyi	Grevy's zebra	Hindgut fermenter	354	101	43.0	50.18	45.89	1.692
Equus hemionus kulan	Asian wild ass	Hindgut fermenter	174	104	50.0	49.86	45.85	0.946
Equus quagga chapmani	Plains zebra	Hindgut fermenter	329	105	46.0	48.46	45.40	1.499
Equus zebra hartmannae	Mountain zebra	Hindgut fermenter	272	119	43.0	49.46	41.80	1.142
Ceratotherium simum	White rhinoceros	Hindgut fermenter	1724	63	64.0	51.10	48.42	10.048
Rhinoceros unicornis	Asian rhinoceros	Hindgut fermenter	1852	67	67.0	52.43	50.96	5.227
Elephas maximus	Asian elephant	Hindgut fermenter	2665	85	50.0	46.38	44.86	7.020
Loxodonta africana	African elephant	Hindgut fermenter	2873	86	52.3	45.15	43.44	7.285

[1]data from Foose (1982)
[2]data from Fritz et al. (2009)

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414 Table 1. Phylogenetic signal and scaling with body mass of mammalian digestive physiology
415 parameters
416

Parameter	---------- Phylogenetic signal ----------				Correlated evolution	
	λ	Lh (λ)	Lh (λ=0)	P-value	Lh (λ,r=0)	P-value
Digesta retention	0.95	21.8	8.85	<0.0001	21.3	0.32
Mean particle size	0.97	-4.3	-16.1	<0.0001	-10.0	0.0007
Fibre digestibility	0.99	34.9	20.3	<0.0001	34.6	0.44
Relative organic matter intake	1.02	17	-0.6	<0.0001	16.5	0.32
Relative digestible organic matter intake	1.00	15.1	1.85	<0.0001	14.3	0.21

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418 Notes: Tests of phylogenetic signal compare likelihoods (Lh) for a model in which λ is
419 estimated to a model in which λ was forced to equal zero; in both models, we estimated the
420 correlation between traits. For tests of correlated evolution (last two columns), we further
421 developed a model in which λ was estimated and the covariance between traits was forced to
422 equal zero. In this case, we compared the model to the likelihood score from λ estimated, i.e.,
423 Lh (λ), in a likelihood ratio test.
424

Table 2. Multiple linear regression according to Fibre digestibility (%) = a + b logBody mass + c Relative organic matter intake + d Digesta retention time + e logFaecal particle size. A PGLS model with λ=0 is equivalent to a non-phylogenetic test.

Factor	PGLS (λ=0)		PGLS (λ=1)	
	Beta	p	Beta	p
Body mass	0.034	0.17	0.003	0.91
Relative organic matter intake	-0.011	0.79	-0.041	0.57
Digesta retention time	0.39	<0.001	0.39	0.0003
Faecal particle size	-0.07	<0.001	-0.063	0.027

Table 3. Multiple linear regression according to Relative digestible organic matter intake = a + b logBody mass + c Relative organic matter intake + d Digesta retention time + e logFaecal particle size. A PGLS model with λ=0 is equivalent to a non-phylogenetic test.

Factor	PGLS (λ=0)		PGLS (λ=1)	
	Beta	p	Beta	p
Body mass	0.018	0.57	0.016	0.68
Relative organic matter intake	1.03	<0.001	1.00	<0.001
Digesta retention time	0.181	0.001	0.22	0.071
Faecal particle size	-0.045	0.06	-0.059	0.10

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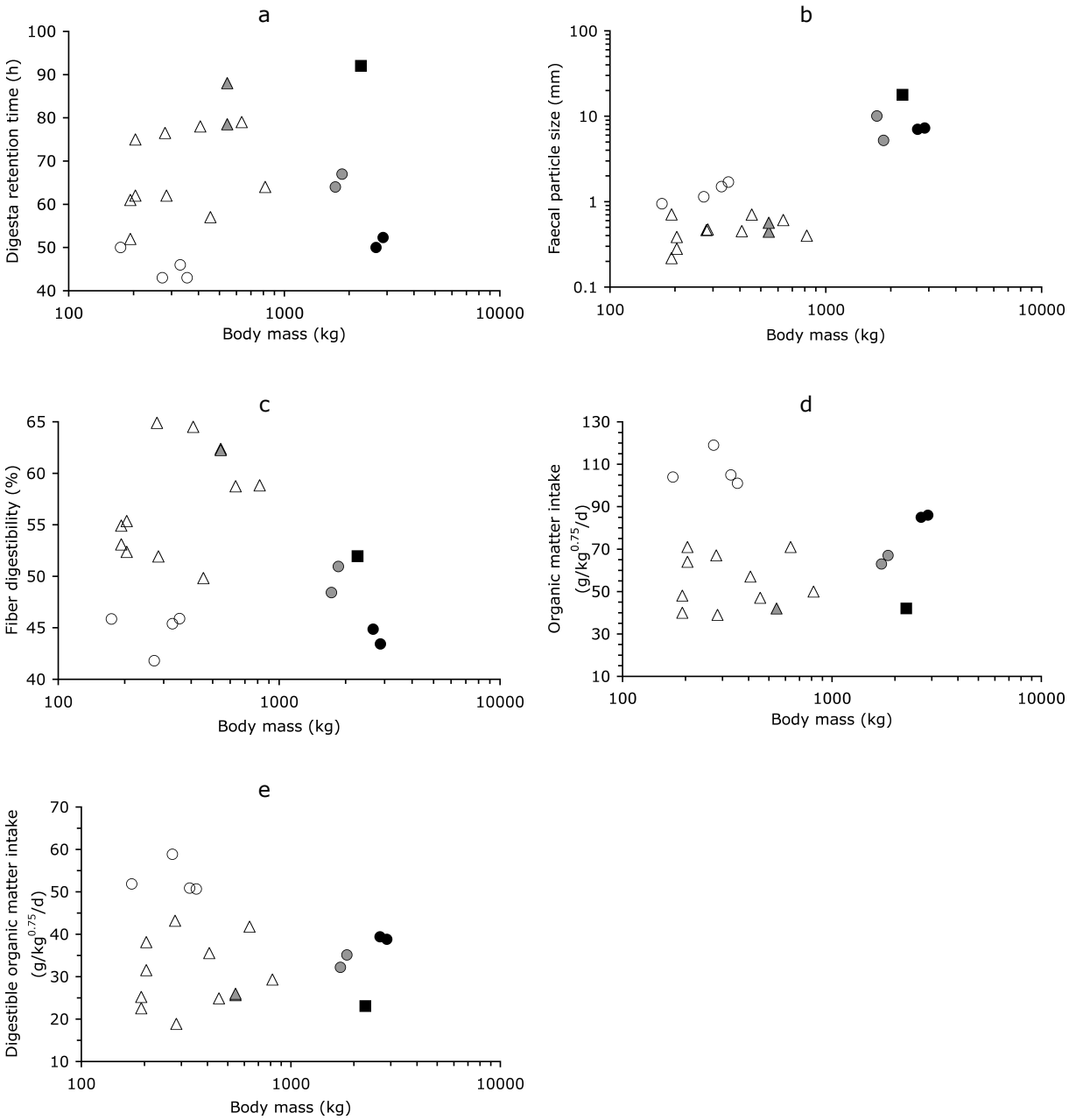

Fig. 1. Correlations between a) body mass and digesta retention time (R=0.18, p=0.429); b) body mass and faecal particle size (R=0.82, p<0.001); c) body mass and fibre digestibility (R=-0.20, p=0.394); d) body mass and relative organic matter intake (R=-0.06, p=0.801); e) body mass and relative digestible organic matter intake (R=-0.13, p=0.563) in large mammalian herbivores (ruminants: open triangles = true ruminants, grey triangles = camelids; nonruminant foregut fermenter: black square = hippopotamus; hindgut fermenters: open circles = equids, grey circles = rhinoceroses, black circles = elephants; statistics for raw data; results of maximum likelihood [PGLS] methods in Table 1)

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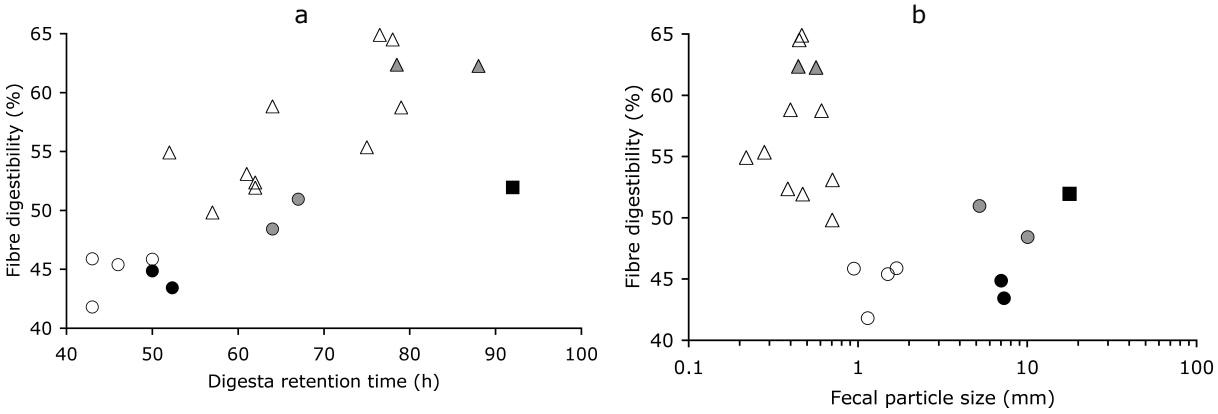

Fig. 2. Correlations between a) digesta retention time and fibre digestibility (R=0.77, p<0.001); b) faecal particle size and fibre digestibility (R=-0.56, p=0.009) in large mammalian herbivores (ruminants: open triangles = true ruminants, grey triangles = camelids; nonruminant foregut fermenter: black square = hippopotamus; hindgut fermenters: open circles = equids, grey circles = rhinoceroses, black circles = elephants; statistics for raw data; results of maximum likelihood [PGLS] methods in text)

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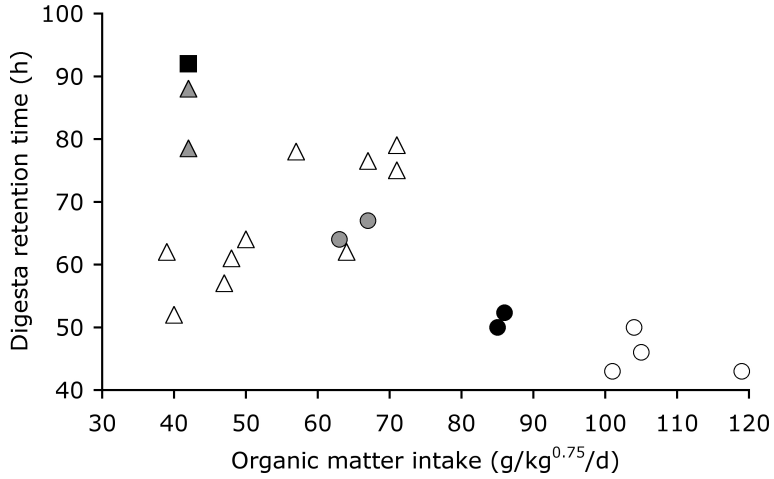

Fig. 3. Correlation between organic matter intake and digesta retention time (R=-0.65, p=0.002) in large mammalian herbivores (ruminants: open triangles = true ruminants, grey triangles = camelids; nonruminant foregut fermenter: black square = hippopotamus; hindgut fermenters: open circles = equids, grey circles = rhinoceroses, black circles = elephants; statistics for raw data; results of maximum likelihood [PGLS] methods in text)

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